The foraging and diet of non-breeding Hooded Plovers *Thinornis rubricollis* in relation to habitat type

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Abstract

Hooded Plovers *Thinornis rubricollis* occupy diverse wetland habitats including brackish, marine and hypersaline systems. I investigated the diet and foraging behaviour of non-breeding adults of this species at three sites that represent the main habitats of this species: 1) a salt-lake in Western Australia, 2) a brackish near-coastal lake in Victoria, and 3) on Victorian beaches. Foraging behaviour and diet was distinctly different between habitat types. Beach birds probed more frequently (40.0% cf. 6.4% of observations; n = 190), had more successes (89.7% cf. 29.2%; n = 177) and foraged slower ($23.9 \pm \text{sd}$ 17.0 s cf. $16.2 \pm \text{sd}$ 7.5 s for ten pecks or probes; n = 192) in comparison with salt-lake birds. Foraging at the brackish lake was slowest of all habitats ($34.1 \pm \text{sd}$ 17.2 s), with the percentage of successful foraging events (81.8%), and those with probes (20.0%), intermediate between the other two habitats (n = 11). Two foraging behaviours ('darting' and 'foottrembling') were recorded only on beaches. Faecal analysis (n = 85) revealed that the diet of coastal Victorian birds was dominated by crustaceans and insects whereas birds at the salt-lake almost exclusively consumed *Coxiella* spp., an endemic gastropod. I also report two new dietary items (insects).

Keywords: foraging ecology, habitat, diet, Coxiella, Hooded Plover, conservation

Introduction

One of the many factors influencing the foraging of birds is features of the prey including spatial distribution, prey type, and energy content (Baker 1974; Iwasa et al. 1981; Sutherland 1982). Natural cycles and events, such as season, day/night and rainfall also affect foraging (e.g., Robert & McNeil 1989; Rompre & McNeil 1994; Weston & Elgar 2000). Other factors that influence foraging include social factors, for example group size and aggression of the birds (Sutherland & Koene 1982; Knight and Knight 1986) and internal factors such as energy reserves or age (e.g., McNamara & Houston 1986). Habitat also is a major influence on foraging ecology: different foraging behaviour and diet has been documented in different habitats (e.g., Van Der Merwe et al. 1992). Habitat-related differences in foraging and diet may be particularly evident in those species that occur in distinctly different habitats.

Food resources are an essential component of a species' habitat, and a good understanding of those resources is desirable when decisions are to be made regarding the management of a species and its habitat. For the Hooded Plover *Thinornis rubricollis*, a threatened species, several processes (e.g., kelp harvesting, inflow of agro-chemicals and other pollution) have the potential to alter the food available to the species (Garnett & Crowley 2000). Human disturbance also disrupts foraging in plovers (Burger 1991, 1994), and may detrimentally affect Hooded Plovers (Schulz & Bamford 1987). An assessment

of the possible impact of these threatening processes on Hooded Plovers requires a good understanding of the foraging ecology of the species. However, with some exceptions (Schulz et al. 1984; Buick 1985; Schulz 1986; Bear 2000; Weston & Elgar 2000), little is known of the foraging behaviour and diet of the Hooded Plover. In particular, the foraging ecology of this species away from ocean beaches is poorly known and virtually unstudied. This is a key information gap for this species in Western Australia (Singor 1999), which is in need of further research to enable appropriate management of the Western Australian population (Raines 2002).

Hooded Plovers occur in two allopatric populations where they use distinctly different habitat types. In both eastern and western Australia, birds use open ocean beaches. In Western Australia, salt lakes close to and far inland from the coast are a major habitat. In eastern Australia, a few birds use near-coastal brackish lakes (Marchant & Higgins 1993). The nature of food resources, diet and foraging could vary between these diverse wetland habitats that range from brackish to hypersaline systems. This paper describes and compares the diet and foraging behaviour of this threatened species in its three main habitat types.

Study areas and methods

Three study areas were sampled. A description of these areas, the population of Hooded Plovers they supported and the study effort, is provided below (key locations are provided in Fig. 3).

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Hypersaline lake

A large aggregation of non-breeding birds was studied at Lake Gore, near Esperance, south-western Western Australia (33°46' S, 121°32' E). This 740 ha hypersaline lake is at the terminus of the Dalyup River and lies four kilometres inland of the Southern Ocean (for more detail, see RIS 2003). The study period extended from 11 to 25 February 1995. During the study period up to 959 Hooded Plovers were recorded simultaneously at the site, which represented a significant proportion (46%) of the estimated western population of the species (Weston & Elgar 2000; Weston et al. 2004) and most other counts (Newbey 1996; Singor 1999) confirm this as the most important site for the western population. During the study period, more males than females were at the lake (Weston et al. 2004). I was unable to make observations at multiple lakes due to the scarcity and unreliable occurrence of Hooded Plovers at other nearby lakes at this time. Thus, I assume this lake is characteristic of other salt lakes used by the species.

Ocean beach

An intensive study of the ecology of Hooded Plovers was conducted from 1995 to 1999 on the south-central coast of Victoria, mostly between Cape Otway (38°45' S, 143°23' E) and Wilson's Promontory (39°04' S, 146°20' E) (Weston 2000). Within this section of coast, most Hooded Plovers occur on sandy ocean beaches. The section of coast sampled is substantial representing roughly 35% of the 1,100 km ocean coastline of Victoria (after Duncan 1982), and holding roughly 40% of the State population (6% of the total estimated eastern population) of Hooded Plovers (after Weston 2003).

Brackish lake

At one Victorian site (Lake Victoria, near Point Lonsdale [38°17' S, 144°37' E]) Hooded Plovers were regularly observed away from the beach during the study described above. Lake Victoria is a land-locked brackish lake, just behind the coastal dunes several hundred metres from the beach (for a site description see Hewish 2003). I was unable to sample at other near-coastal brackish lakes because the species uses very few of these lakes in eastern Australia, and the occurrence of the species at other brackish lakes is unpredictable. Thus, I assume this lake is characteristic of other brackish lakes used by the species.

Foraging observations

Plovers forage on ground (damp or dry) or in shallow water. They walk or run across the substrate and take prey from on, or just underneath, the surface. The open nature of their habitats combined with conspicuous foraging movements means observations reveal useful information on foraging behaviour.

Foraging observations were collected according to the procedures detailed in Weston & Elgar (2000). Each bird was observed through a telescope from a hidden position. The following were recorded: the time taken to make ten bill movements (pecks or probes), the number of bill movements that were successful, and the number of probes. Sometimes 1 was not confident that all these parameters had been measured accurately (e.g., if a foraging bird turned away from view). Such data points

were excluded from the analyses. Foraging events that were collected from juveniles or leg injured birds, or those that were interrupted by non-foraging behaviours were excluded. Juvenile shorebirds may forage at different speeds or efficiencies to adults (e.g., Burger & Gochfeld 1985), and less efficient foraging is likely for leg injured birds; there were not enough observations of juveniles or leg injured birds across habitats to allow comparisons, so they were excluded from the dataset.

In Western Australia, birds were selected for observations haphazardly, but the large number of birds at the lake meant that foraging events could be reasonably considered independent data points (Weston & Elgar 2000). Here, I have selected for analysis only those foraging events that occurred during dry weather (n = 140), because a major rainfall event that occurred later in the data-gathering period affected foraging behaviour and was possibly unusual (Weston & Elgar 2000).

Data gathered in eastern Australia included observations of breeding birds foraging in pairs or those attending eggs or chicks. In order to produce data comparable to that collected in Western Australia for this analysis, I selected foraging events from non-breeding flocks. In Victoria, most birds under observation were colour-banded and so could be individually recognised. However, the amount of data available for each bird varied from a single foraging event to 143 events. Thus, the first foraging event recorded for each bird was selected for analysis to ensure all data points were independent (n = 41, beaches; n = 11, Lake Victoria).

Beach habitat was classified into five levels: (1) rock platforms; (2) lower beach, which had constant wave wash and was exposed between waves; (3) mid-beach, which was covered by the previous nocturnal tide and was flat and wet; (4) upper beach, which was the area above the previous nocturnal high tide mark (it was clearly differentiated from the mid-beach because it was dry and was usually covered with numerous footprints and tracks; beach-cast seaweed tended to be at least partially covered by sand in this level, whereas in the mid-beach it tended to be wet and uncovered); and, (5) foredunes and dunes, which began at the lowest beach vegetation or where there was a substantial change in slope (whichever occurred lower), and extended landward.

Diet

During all foraging observations, and field work in general, I opportunistically recorded any prey that I could identify. Faecal samples were collected opportunistically in such a way so as not to disturb foraging birds under observation. All faecal samples collected were seen to be defecated by Hooded Plovers, so samples were not confused with faeces of other shorebird species that often foraged near Hooded Plovers. Faecal samples in Western Australia were collected before the major rainfall event that occurred at the end of the study period (Weston & Elgar 2000). No faecal samples were collected from Lake Victoria.

Faecal samples were small ($0.473 \pm sd~0.188$ g, n = 20 dried faeces from Lake Gore) and were stored in alcohol in labelled vials. In the laboratory, the samples were

sorted and examined under a binocular microscope. Remains in faecal samples were identified to the level of class, although I was able to identify some prey to family and species level. I used faecal analysis on a reasonably large number of samples to determine the proportion of samples containing different prey types. This approach allowed me to characterise diet in the different habitats. The aim of the faecal analysis was to characterise diet rather than describe the diet of individual birds in high detail.

Small reference samples of benthos were collected at Lake Gore and at a similar lake (Station Lake, near Esperance [33°48′ S, 121°56′ E]), where Hooded Plovers were also seen foraging. These were not intended to describe prey populations, but to aid identification of prey items in the faecal samples. Some intact items of potential prey were sun-dried and weighed on a digital balance in the laboratory.

Comparisons and analysis

Here, I attribute observed differences in foraging behaviour and diet to habitat. However, the slight morphological differences between eastern and western Hooded Plovers (Marchant & Higgins 1993), and the fact that the populations are sometimes considered distinct subspecies (e.g., Garnett & Crowley 2000), represents a potentially confounding covariable. My aim was not to examine the influence of morphological variation on foraging, but to broadly characterise foraging and diet in major habitat types.

It was not possible to sample Hooded Plovers from replicate lakes, because of logistical constraints due to the relative rarity of the species and the unpredictable occurrence of the species in lake habitats. Thus, I assume that the lakes sampled are representative of a particular habitat type.

Results

Foraging behaviour

Summary statistics of foraging behaviour (n = 192 foraging events) for each of the three habitats are presented in Table 1. Differences were found in all parameters measured, such that at Lake Gore birds foraged more rapidly but had fewer successes and fewer probes compared with eastern birds. Victorian beaches were the site of the greatest number of probes and successes.

Two foraging behaviours seen on Victorian beaches were never seen at the lakes. These were 'darting' (rapid pursuit of jumping prey involving a number of rapid changes in direction) and 'foot-trembling' (the rapid vibration of the foot on the substrate, after Schulz 1997). Both behaviours were infrequent, being recorded on 0.9% (n = 1636 foraging events where the presence or absence of this display was noted) and 1.0% (n = 1662) of foraging events respectively. These behaviours did not occur in all levels of the beach (Fig. 1).

Die

I quantified the proportion of faecal samples that contained different kinds of prey (Fig. 2). Eastern beachdwelling Hooded Plovers had a more varied diet in comparison with the birds from Lake Gore, although the average number of prey classes identified per faecal sample were similar (salt-lake, $1.0 \pm \text{sd}\ 0.2$, n = 50; beach, $1.1 \pm \text{sd}\ 0.7$, n = 35). While both beach and salt-lake birds consumed insects, crustaceans and gastropods, these prey types occurred in distinctly different frequencies in my samples (contingency analysis, $\chi^2 = 75.2$, df = 2, P < 0.001). Crustaceans and insects dominated the diet of beach foraging birds in Victoria, whereas they were present in low frequencies in the faeces of salt-lake

Foraging behaviours in the different habitats.

Parameter	Salt-lake (Lake Gore)	Brackish Lake (Lake Victoria)	Beaches (Victorian Beaches)	Comparison
Time to make ten bill movements (in seconds)	16.2 ± sd 7.5 (6.7 – 62.0; n = 140)	34.1 ± sd 17.2 (18.3 – 78.4; n = 11)	23.9 ± sd 17.0 (4.8 – 87.7; n = 41)	One-way ANOVA on logged data, $F_{2.189} = 17.286$, $P < 0.001$
Number of successes (median)	0 (0 – 4; n = 137)	2 (0 – 7; n = 11)	(0-9; n=29)	Excluding zeros, Kruskal-Wallis Statistic = 8.162 , df = 2 , P = 0.017
Number of probes (median)	(0-3; n = 140)	(0-4; n=10)	0 (0 – 10; n = 40)	*Excluding zeros, Mann-Whitney U = 25.5, P = 0.007
Percentage of events with successes	29.2	81.8	89.7	$^{**}\chi^2 = 40.745,$ df = 1, $P < 0.001$
Percentage of events with probes	6.4	20.0	40.0	$\chi^2 = 29.052$, df = 2, P < 0.001

Table 1

only two birds from Lake Victoria made probes and Lake Victoria birds were excluded from the analysis.

^{**} eastern birds were pooled so that enough expected frequencies exceeded five to allow valid analysis.

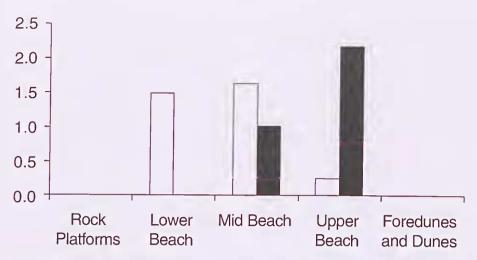


Figure 1. The occurrence (percentage of foraging events) of 'darting' and 'foot-trembling' at different levels on Victorian beaches. 'Darting' (solid bars) and 'foot-trembling' (open bars) are shown.

foraging birds. While gastropods were consumed on beaches, they dominated the faecal samples collected from the salt-lake (Fig. 2).

Snails of the native genus Coxiella dominated the diet of birds at Lake Gore; this snail is visually conspicuous here, its shells forming extensive deposits. All gastropods from Lake Gore shown in Figure 2 were apparently Coxiella spp. Identification of some Western Australian forms of Coxiella is difficult, with some specimens displaying characteristics of several recognised taxa (S. M. Slack-Smith in litt.). Additionally, the shells in the faecal samples were highly fragmented, making identification difficult. A subset of three faecal samples was forwarded to S. M. Slack-Smith (Western Australian Museum) in an attempt to identify the species of Coxiella in the faecal samples. Two faecal samples from Lake Gore contained only *C. striatula*, however one sample also contained a smooth shelled species (either C. glabra or the young of C. pyrrhostoma). Details of the prey items identified are given in Table 2.

The reference sample from Lake Gore contained only Coxiella striatula but the reference sample from Station

Lake contained *C. striatula*, *C. pyrrhostoma*, *C. glabra* and *C. exposita*. A preliminary identification of some shells from Lake Gore suggested that *C. exposita* was also present (Singor 1999). Intact *C. striatula* in the reference sample weighed $0.005 \pm sd \ 0.001 \ g \ (0.004 - 0.006; \ n = 4)$. At Lake Gore, small black seeds and dead insects (flying and terrestrial) were located on the substrate during the study period. The seeds weighed $0.003 \pm sd \ 0.001 \ g \ (0.001 - 0.007; \ n = 7)$. These seeds appeared to be the type consumed by Hooded Plovers (see below).

I also recorded any prey I could identify as I watched foraging birds (Table 2). Birds were seen taking black seeds from the surface of the substrate of Lake Gore. In Victoria, very few prey items were identified despite extensive observations (including over 15 hours of foraging event recordings). However, I did observe: (1) a pair pulling Polychaete worms from a mudflat beside a tidal creek, (2) several observations of plovers chasing and consuming stranded moths, (3) an adult consuming a sand fly that had been killed by the observer, and (4) several observations of birds chasing and eating sand-hoppers (see Table 2).

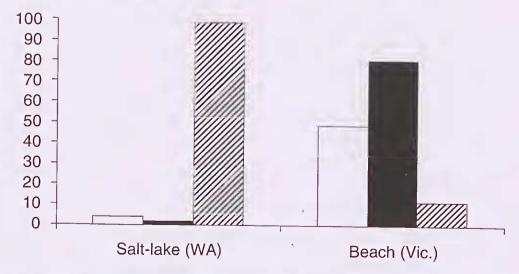


Figure 2. The percentage of faecal samples containing different prey types (n = 35 for beaches; n = 50 from Lake Gore). Insecta (open bars); Crustacea (solid bars); and Gastropoda (hatched bars).

Table 2

The dietary items identified from Hooded Plover faecal analysis and observations. Items not listed in Marchant & Higgins (1993) are marked with an asterisk.

Habitat	Orde r	Family (finer classifications are provided where possible)	
Beach (Vic.)	Gastropoda Polychaeta Crustacea	(unidentified). (unidentified). Amphipoda (Eusiridae, Hyalidae).	
	Insecta	Isopoda. Coleoptera (Staphilinidae). Hemiptera. Diptera (Sdvatiomyidae, Tabanidae). Lepidoptera. * Hymenoptera. *	
Salt-lake (WA) Gastropoda Crustacea Other		Pomatiopsidae (Coxiella spp.) (unidentified). Seeds (unidentified).	

Discussion

This study has detected substantial differences in the foraging behaviour and diet of Hooded Plovers inhabiting diverse wetland habitats in eastern and western Australia.

Behaviour

Hooded Plovers foraging on beaches use some specific behaviours ('darting' and 'foot-trembling') not observed in lake habitats. These behaviours are probably aimed at capturing prey that occurs in beach rather than lake habitats. I suggest that these behaviours are used when foraging for sand-hoppers (Schulz 1997; pers. obs.). Every time I observed these behaviours and could identify the prey item, the birds were feeding on sand-hoppers. This is also supported by the finding that these behaviours did not occur in all levels of the beach but were apparently concentrated in zones of the beach with abundant sand-hoppers (see Schulz *et al.* 1984; Schulz 1997).

Other behaviours (pecking and probing) are used in all habitats but at different rates. Eastern (non salt-lake) birds frequently probed, suggesting that prey that lives below the surface of the substrate were taken often, perhaps contributing to the more diverse diet of those birds. One possible explanation for the lower rate of probing at the salt-lake is that the substrate was harder there, however, unpublished data suggest that hardness was similar to that on Victorian beaches (penetration of a metal rod dropped from waste height: Lake Gore, 5.5 ± sd 2.7 cm, n = 6; Victorian beach, $4.3 \pm sd 1.9$ cm, n = 6). Birds on the beach foraged slowly in comparison with the birds foraging at the salt-lake, yet they achieved a higher success rate. I have no significant time budgeting data from the salt lake, but it may be that salt lake birds have to forage for longer each day to meet their energy requirements (i.e., to obtain sufficient successes). Alternatively, Coxiella may be a particularly profitable prey in comparison with the prey consumed by beach dwelling birds. The difference in the speed of foraging

may reflect different prey availability or detectability. The digestion of *Coxiella* may also be a limiting factor (perhaps because of the hard shell), and may require careful size selection of prey to be consumed.

A comparison between brackish and salt lake foraging birds reveals differences in foraging behaviour, although the low sample size from the brackish lake means the results must be interpreted cautiously. Birds at the brackish lake foraged more slowly but achieved a higher success rate than birds foraging on the salt-lake. I know nothing of the diet of Hooded Plovers at the brackish lake, but the foraging habitat was unusual. For example, some birds foraged among saltmarsh, and others on artificial shellgrit spits (M. A. Weston unpublished data). It is possible that birds at the brackish lake used the site primarily as a roost site or disturbance refuge, and foraged only occasionally. Colour-banding indicates that birds at Lake Victoria also forage on the beach (M. A. Weston unpublished data), and so foraging at the lake may represent opportunistic foraging at a site used mainly for non-foraging activities. In contrast, salt-lakes are the site of significant foraging (Weston & Elgar 2000).

Diet

I observed two non-marine prey items (ants and moths) apparently not previously known from the diet of Hooded Plovers (see Marchant & Higgins 1993). Beachcast wrecks of moths occur infrequently in Victoria, but ants are common in dunes (pers. obs.). These items emphasise the opportunistic nature of foraging on beaches.

Faecal analysis has the advantage of being non-intrusive, but soft prey items may not be detectable: prey are usually fragmented and hence difficult to identify, and the number of prey items in a sample cannot be determined (Ford et al. 1982). Nevertheless, faecal analysis does provide useful information on diet, including comparative information of the type generated by this study. I uncovered dramatic differences in the diet of Hooded Plovers foraging on eastern beaches and western salt-lakes. Eastern beaches offered a diverse diet in comparison with the salt-lake. Crustaceans were the main component of the beach diet while gastropods (Coxiella spp.) overwhelmingly dominated the diet of Hooded Plovers at the salt lake.

Coxiella spp. is suspected of being an important component of the diet of inland dwelling Hooded Plovers in Western Australia, and in the lakes of the Coorong and on Kangaroo Island, South Australia (Buick 1985; Marchant & Higgins 1993; Baxter 1995; Johnstone 1998; Singor 1999; Garnett & Crowley 2000). This study has confirmed the predominance of Coxiella in the diet of lake-inhabiting Hooded Plovers in Western Australia. Hooded Plovers move from Lake Gore at least to other lakes (e.g., Weston 2002), so further sampling of additional lakes may help confirm the role of Coxiella in the diet.

It has been speculated that *Coxiella* may be a critical component of the habitat for Hooded Plovers in the lake systems of Western Australia (Singor 1999). The distribution of *Coxiella* corresponds with some areas where Hooded Plovers occur away from the coast, particularly in Western Australia (Fig. 3). However, the correspondence of Hooded Plover and *Coxiella*

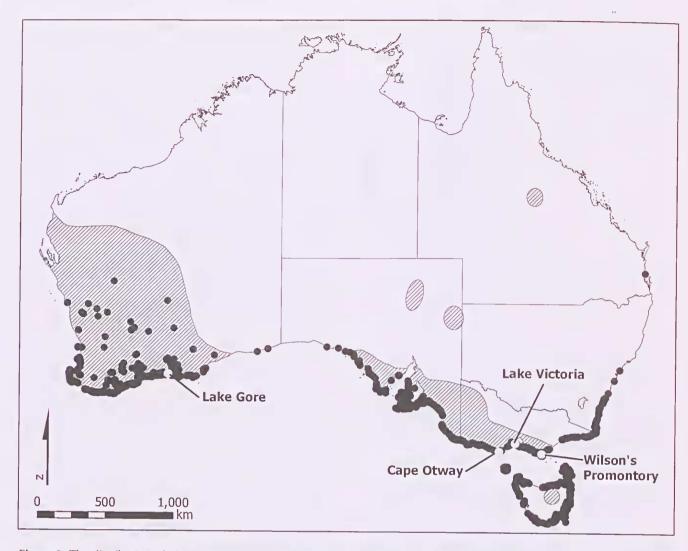


Figure 3. The distribution of Hooded Plovers and Coxiella spp. (data are from Williams and Mellor 1991 and Barrett et al. 2003 [extracted April 2007]). The limits of Coxiella spp. are shown as hatched areas, while distributional records of Hooded Plovers are shown as solid dots. Key locations are shown as white dots and are labelled.

distributions is only partial with some areas where Coxiella occurs not supporting Hooded Plovers, most notably non-coastal areas of Victoria, northern South Australia and in Queensland. This is particularly interesting in the case of subcoastal Victoria, because a considerable population of Hooded Plovers occur on the coast there, but apart from a few minor occurrences, they do not use the subcoastal wetlands. In South Australia, a few reports suggest that Hooded Plovers will use subcoastal lakes, including salt-lakes (e.g., Bransbury 1990), and it would be interesting to determine the diet of those birds. Bird distributions are determined by a complex set of biological and non-biological variables. However, the apparent strong link between predator and prey in a major habitat in Western Australia, suggests the pattern of co-occurrence there may be ecological in

While the presence of *Coxiella* may not fully explain the inland distribution of Hooded Plovers, the results of this study suggest *Coxiella* plays an important role in the foraging ecology of this species. Sympathetic management regimes that maintain *Coxiella* populations, such as maintenance of high water quality, are likely to be important for the effective management of Hooded

Plovers inhabiting lakes. The management of water quality in habitat of the western Hooded Plover may be an especially important issue given the widespread application of superphosphate and rising river salinity over several decades in the catchments of Lake Gore and other key lakes in Western Australia (WRC 2002; RIS 2003).

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